

the ischnoceran Mallophaga since the same species of lice were found on both hosts. *Buceronirmus* new species 1 and *Paroncofhorus javanicus* (Rudow) were found on both subspecies of *Rhyticeros undulatus* and on *R. plicatus subruficollis* (Elbel, unpublished). If these two hosts represent distinct species, the ischnoceran genera *Buceronirmus* and *Paroncofhorus* have not speciated as rapidly as the amblyceran genus *Chapinia*. Clay (1957) stated that rates of speciation have been so different in the Amblycera and Ischnocera that comparisons of these rates on the same host group have little value. If the hosts, *R. undulatus* and *R. p. subruficollis*, represent the same species, the amblyceran lice, *Chapinia boonsongi* and *C. hirta*, must have been sympatric species on both host populations. Suppose that *C. boonsongi* became extinct on *R. p. subruficollis* and that *C. hirta* became extinct on *R. undulatus*. Then the two forms of *Rhyticeros* would be closer than their Mallophaga indicated. Clay (1949) was the first to mention this type of distribution. The fact that two species of *Chapinia* have not been found on any hornbill (Elbel 1967) would seem to suggest that sympatric pairs were not involved and that the hosts should remain as distinct species. However, as mentioned by Clay (1957), the evidence of relationship provided by one genus of Mallophaga is less convincing than if more genera were involved.

In the Australian region a different relationship was found. *Buceronirmus* new species 2, *Chapinia hirta*, and *Paroncofhorus javanicus* were found on all subspecies of *Rhyticeros plicatus* (Elbel, unpublished). The speciation that has occurred in the *Buceronirmus* would suggest that the Australian forms of *R. plicatus* have become isolated from the Oriental *R. p. subruficollis* and thus should be specifically distinct; but again the evidence of relationship provided by one genus of Mallophaga is less convincing than if more genera were involved. Clay (1949) stated that if one of the louse species of a host species with an extensive range became extinct in the middle portion of that range, the two louse populations at either end would be isolated, and that by the time the louse species again spread throughout the population of the host, some kind of sexual isolating mechanism might have developed in one of the louse populations. If this were the case, one would expect to find both

species of *Buceronirmus* on the same subspecies of *R. plicatus* somewhere within its range. Since this has not been found, perhaps critical ornithological work will show that *R. p. subruficollis* is reproductively isolated and should be separated specifically from the subspecies of *R. plicatus* in the Australian region.

In these two examples the mallophaga afford a suggestion as to the distinctiveness of the host *Rhyticeros plicatus subruficollis*. Mallophaga are considered only as contributory evidence to the morphological and biological data from the host birds (Elbel and Emerson 1959).

In summary, Mallophagan evidence suggests that *subruficollis* is not a synonym of *Rhyticeros undulatus* as Sanft (1953) thought, and may in fact, be specifically distinct from *plicatus*, of which *subruficollis* has been considered a subspecies by recent authors.

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EXTENSION OF ZONE OF SYMPATRY OF *QUISCALUS MEXICANUS* AND *Q. MAJOR*

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In 1960 the zone of sympatry between the Great-tailed Grackle (*Quiscalus mexicanus*) and the Boat-tailed Grackle (*Q. major*) was known to extend from near Green Lake and Port Lavaca, Calhoun County, Texas, eastward through the Houston-Galveston area to the vicinity of Sulphur, western Calcasieu Parish, Louisiana (Selander and Giller, *Condor* 63:33-38, 1961). Distributional data from the early literature suggested that *Q. mexicanus*, extending its range along the Gulf coastal plain from southern Texas, reached the Houston-Galveston area between 1912

and 1938, and invaded southwestern Louisiana between 1938 and 1959.

In 1960 no breeding records of *Q. mexicanus* were available from localities east of Calcasieu Lake and Calcasieu River (Selander and Giller, op. cit., figs. 2, 3). Apparently the eastward movement of *Q. mexicanus* is continuing, for on 29 and 30 May 1968 we found it at Grand Lake, Cameron Parish, and in the Gibbstown-Bell City area, eastern Calcasieu Parish, 21 mi. SE of Sulphur, where it was nesting in mixed colonies with *Q. major* in patches of pine between farms. Specific localities of colonies are: 5 mi. E of Grand Lake; points 4.7, 5.0, 6.0, 6.3, and 6.7 mi. N of Gibbstown; and 7.5 mi. W of Bell City on state road 14. Since *Q. mexicanus* was common in the Gibbstown-Bell City area, it seems probable that its range extends even farther east in the coastal prairie region toward Lake Arthur.

A total of 134 adult and first-year specimens of *Quiscalus* was collected east of Lake Calcasieu for studies of variation in biochemical characters. All

TABLE 1. Measurements of *Quiscalus* from the Gibbstown-Bell City area, Louisiana.

Species	n	Measurements (mm)									
		Wing length		Tail length		Bill length		Bill depth		Tarsus length	
		\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Adult male											
<i>Q. major</i>	13	174.4	3.80	175.3	6.34	30.76	1.111	11.68	0.400	47.38	1.344
<i>Q. mexicanus</i>	11	187.9	4.28	209.2	10.55	31.72	1.618	12.54	0.548	47.43	1.040
Adult female											
<i>Q. major</i>	43	136.9	2.64	131.0	4.47	25.22	0.919	9.56	0.197	39.08	0.881
<i>Q. mexicanus</i>	49	144.9	2.25	147.1	5.16	24.61	0.846	10.06	0.283	38.76	1.142

specimens were identifiable to species on the basis of eye color alone (see Selander and Giller, op. cit.: 43), and none showed evidence of mixed ancestry in any character. Measurements of adult male and female specimens, supplementing those presented graphically by Selander and Giller (op. cit.), are given in table 1.

The continuing eastward extension of the range of *Q. mexicanus* into that of *Q. major* provides an opportunity to study the ecological interactions of

closely related species which overlap in niche requirements. We predict that *Q. mexicanus* will eventually reach the Atlantic coast states, becoming broadly sympatric with *Q. major*, and, in the process, replacing that species in upland habitats. This research was supported by the U. S. Public Health Service, Institute of General Medical Sciences (GM-15769).

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THE NUMERICAL RESPONSE OF WOODPECKERS TO INSECT PREY IN A SUBALPINE FOREST IN COLORADO

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Several field workers have reported concentrations of woodpeckers associated with insect prey attracted to trees killed by floods and fires (Yeager 1955; Blackford 1955) or with epidemics of forest insects (Massey and Wygant 1954; Baldwin 1960). Several other workers reported significant differences in numbers of woodpeckers inhabiting forests supporting endemic populations of forest insects and numbers of woodpeckers inhabiting similar forests supporting epidemic populations of forest insects (Amman and Baldwin 1960; Otvos 1965). None of these investigators observed the numerical response—the changes in densities of predators in response to changes in densities of prey (Holling 1959)—of woodpeckers to an increasing food supply, nor did they attempt to explain the differential response of each species in terms of foraging adaptations. The purpose of this paper is to present such a report.

METHODS

The study was conducted between July 1962 and August 1965 in a subalpine forest in the vicinity of Deadman Lookout in the Red Feather District of the Roosevelt National Forest, Larimer County, Colorado. The vegetation of the study area is dominated by Engelmann spruce (*Picea engelmanni*), subalpine fir (*Abies contorta*), and lodgepole pine (*Pinus contorta*). The woodpeckers studied included Northern Three-toed (*Picoides tridactylus*), Hairy (*Dendrocopos villosus*), and Downy (*D. pubescens*).

I censused woodpeckers by means of census plots (Amman and Baldwin 1960) and census strips (Davis 1963). Woodpeckers were so sparse that, to

obtain a sufficient number of observations to adequately estimate densities, censusing was conducted during all daylight hours. To determine if birds were more active during a given time of day, I frequently censused a plot three times daily (early morning, around noon, and late afternoon) and statistically compared the results by means of contingency tests. I tested results only from those days that had consistent weather patterns throughout the whole day.

A small fire in October 1962 killed or damaged approximately 10 acres of trees within the study area. Censuses were conducted through portions of the burn, but no special effort was made to census the burned area until I realized in July 1964 that woodpeckers were feeding on bark beetles attracted to the fire-damaged trees. Although no attempt was made to census insects attracted to the trees, periodic examinations were made to identify the species of insects attracted to the trees and to gain an impression of their relative abundance.

I studied the foraging behavior of individual woodpeckers by noting the species and condition (living or dead) of each tree utilized, and the foraging site occupied by each bird in these trees. I timed each bird with a wrist watch as it foraged in different trees and in various sites.

RESULTS AND DISCUSSION

Prey populations. Even though bark beetles were not censused, their presence and high abundance during the fall of 1964 were readily apparent from entry holes in the bark, boring dust at the bases of fire-damaged trees, and larval galleries exposed by the flaking activities of woodpeckers. *Ips pilifrons* was the most abundant bark beetle in the trunks and larger branches, and *Pityophthorus* sp. the most abundant in the smaller branches and twigs of fire-damaged Engelmann spruce and lodgepole pine. Subalpine fir was not checked for insects because the trees were heavily laden with pitch and there was little woodpecker activity on them.

The decline in abundance of insect prey during the spring of 1965 was equally apparent. By June almost all of the bark on the fire-killed spruce and

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